# PREDATORY GASTROPODS AND THEIR ACTIVITIES IN THE BLACKDOWN GREENSAND (ALBIAN) OF ENGLAND

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ABSTRACT. The silicified Blackdown Greensand fauna of the Albian in south-west England affords an opportunity for a quantitative assessment of a rich and diverse Cretaceous molluscan fauna. Among its Meso- and Neogastropoda are species of naticids and muricids, as well as numerous Opisthobranchia, all of which today are active predators upon invertebrate prey. Drill holes (amongst the earliest yet recorded) into shelled prey provide evidence of their feeding activities. Analysis of the prey preference and drilling behaviour of two of these predator groups indicates that they were essentially similar to those of their living relatives, but predation rates are significantly lower than in either Cenozoic, or Recent faunas.

PERHAPS one of the most notable events affecting marine benthic faunas during the Mesozoic was the appearance and radiation of those groups of animals which today are the major predators in such habitats, in particular teleost fish, crustaceans, and both prosobranch and opisthobranch gastropods (Vermeij 1977). By comparison with their present-day counterparts, we may assume that the activities of these predators had profound effects upon the behaviour and adaptations of prey organisms and upon the structure and organization of benthic communities (Vermeij 1977; Taylor 1981; Hughes 1980a; Bayne 1981).

Gastropods are perhaps the most diverse group of marine predators living today and they experienced a massive evolutionary radiation during the late Cretaceous (Taylor *et al.* 1980), and probably the great range of diets and feeding adaptations associated with this group were largely established at that time. The radiation apparently began in Aptian/Albian times followed by a near exponential increase in diversity, so that by the end of the Cretaceous most of the present-day families can be recognized.

The feeding habits of fossil gastropods can usually only be surmised from a comparison with their living relatives. However, it is well known that three families of prosobranch gastropods contain species which feed by drilling holes into shelled prey; the Naticidae and Muricidae mainly drill into molluscs, whilst the Cassidae bore into echinoids (Carriker and Yochelson 1968; Bromley 1981; Hughes and Hughes 1981). The predatory shell-drilling habit has also been attributed, by various authors at various times, to species in other prosobranch families, namely the Cymatiidae, Ficidae, Tonnidae, Nassariidae, and Buccinidae; but as far as we are aware, there are no authenticated observations of shell drilling in these families.

Although holes resembling those made by predatory gastropods are found throughout the fossil record (Bromley 1981 and references) it is generally considered that holes having the morphological characteristics of those drilled by predatory gastropods and occurring in some abundance are not found before the upper Cretaceous (Fischer 1962a; Sohl 1969; Carriker and Yochelson 1968; Dudley and Vermeij 1978; Taylor *et al.* 1980). Although occasional holes which resemble those produced by naticid drilling may be found in pre-Cretaceous fossils, they are usually uncommon and little can be said about them. Therefore, although it is probable that shell drilling by gastropods began before the Albian, we believe that the earliest known fauna in which convincing gastropod drill holes are common, is that of the Blackdown Greensand (Albian) of Devon. The holes are relatively abundant, closely resemble those made by present-day naticids and muricids, and occur in similar positions on the predated shells. Moreover, gastropod species referable to these two drilling families are present in

the fauna. Stanton and Nelson (1980) suggested that the drilling habit was a new mode of predation for naticids at the beginning of the Cainozoic, but it is clear that this habit was established at least fifty to sixty million years earlier.

A growing number of studies have documented the drilling activities of naticid and muricid gastropods during the Cainozoic, examining either their distribution in whole assemblages (Adegoke and Tevesz 1974; Hoffman *et al.* 1974; Robba and Ostinelli 1975), or in individual taxa (Thomas 1976; Dudley and Vermeij 1978; Fischer 1962*b*, 1963; Kitchell *et al.* 1981). However, apart from the data on *Turritella* from the Campanian (Dudley and Vermeij 1978) there are no quantitative data on gastropod drilling predation found in Cretaceous faunas. Therefore we have taken the opportunity to locate the older collections made from the Blackdown Greensand to examine the evidence of drilling and describe the activities of predatory gastropods in the fauna, which on current knowledge seems to be very early in the history of such predation. The gastropods in this fauna show considerable diversity, including many species whose living relatives are carnivores and predators, and consequently in this study we also assess the status, relationships, and relative abundance of such gastropods and consider their possible feeding habits.

The activities of the shell-drilling taxa are documented in terms of prey preference, with some evidence of size selection, feeding behaviour, and the possible effect upon the palaeocommunities. The data from this study may contribute information to support or contradict various hypotheses which have been proposed concerning the development of drilling predation. These hypotheses include:

(*a*)  Predation intensity has increased from the Mesozoic to the Cainozoic (Vermeij 1977; Dudley and Vermeij 1978).

(*b*)  There has been a shift in prey preference by drilling gastropods from mainly gastropods in the early Cainozoic to mainly bivalves in the late Cainozoic and Recent (Adegoke and Tevesz 1974).

(*c*)  Predators may have become increasingly efficient in prey capture and drilling behaviour; for instance, Stanton and Nelson (1980) suggest that even in the Eocene, the wide range of prey and incidence of cannibalism indicate lack of efficiency.

THE BLACKDOWN GREENSAND AND ITS FOSSILS

The Cretaceous outlier of Blackdown Greensand is recognized from published accounts (Downes 1882; Jukes-Browne and Hill 1900) as forming a sequence of more than 30 m of sand and layers of cherty sandstone concretions in North Devon. It is dated as upper Albian on the basis of the many ammonites in the fauna, all of which belong to the *Mortoniceras inflatum* Zone, with the well-established occurrence of the *Orbignyi* and *Varicosum* Sub-zones (Hancock 1969, p. 66) and the probability of the *Auritus* Sub-zone at the very top (H. G. Owen, pers. comm.). The majority of the fossils occur in the *Varicosum* Sub-zone.

The deposit, together with the majority of its commoner fossils, was first described by Fitton (1836, p. 236) following his visit there in 1825, but both James Parkinson (1811) and James Sowerby (1813, 1814) had earlier described individual fossils from Blackdown.

Downes (1882, p. 75) described how most early collectors had obtained their specimens from the miners and quarrymen. It was not until he and W. Vicary began to collect *in situ* that any real idea as to the occurrence of the remarkable well-preserved silicified fossils was obtained.

With the closure of the mine workings, it is no longer possible to collect from the exposures in the area. Consequently, our study was completely dependent upon the collections made from the Blackdown Greensand in the last century. Several of the most significant of these collections are in West Country museums: the City Museum, Bristol (Miller collection); Royal Albert Memorial Museum, Exeter (Downes collection); and the Somerset County Museum, Taunton (Fox and Williams collections). Other important material occurs at the Sedgwick Museum, Cambridge (Meyer and Wiltshire collections), at the British Museum (Natural History) (Vicary collection), and the Institute of Geological Sciences, London (Sclater collection).

With the considerable disadvantages of museum collections we have very little information concerning which fossils occurred together. We have had to assume that the relative abundance in collections reflects their natural abundance, although it is very probable that collector bias has resulted in the undersampling of the commoner species and also that thin-shelled, fragile species are also under-represented in collections. Fortunately, Downes's

(1882) thorough examination of the sequence at the eleventh hour, dividing it into twelve beds, has enabled us to gain some idea as to the distribution of the silicified fossils typical of the Blackdown fauna. His description of the beds (pp. 80–4) and lists of the fossils (pp. 85–90) provide the only reliable information that we could use in assessing the co-occurrence of species. In the majority of the beds, the fossils occur in clumps and the two valves of bivalves are nearly always joined; the most fossiliferous beds are found in the centre of the sequence with the shells progressively becoming more worn, separated, broken, and mixed above Bed 8. His observations show that various trigoniid species are restricted to certain beds and that the two species of *Glycymerita* do not occur together. *Granocardium proboscideum* is found only in Bed 10; while arcid bivalves are also more frequent in the upper beds. Most specimens of '*Murex*' *calcar* come from the highly fossiliferous Bed 7 and *Turritella granulata* occurs only between Beds 8 and 10. Downes pointedly emphasized that the two species of *Drepanocheilus* co-occur and that the naticid we now recognize as *Forator parkinsoni* is found in Beds 7–10, as are the commoner species of opisthobranchs, whilst *Neithea gibbosa* is characteristic of the uppermost Bed 12.

We have, in addition, a limited number of larger blocks which have survived in museum collections. These have given some idea of faunal association. Most of the molluscs discussed below seem to occur together in the highly fossiliferous Beds 7 and 8.

## THE DEPOSITIONAL ENVIRONMENT OF THE BLACKDOWN GREENSAND

The fauna of the Blackdown Greensand, showing an abundance of aporrhaid and turritellid gastropods together with corbulid and venerid bivalves, would by comparison with Recent communities suggest an offshore, sandy bottom fauna living at water depths of between 15 and 85 metres.

The limited evidence we have indicates that we are discussing several assemblages with many taxa in common. These are what is preserved of fluctuations in faunal composition apparently dependent upon slight variations of the sediment.

Communities dominated by turritellid gastropods are known throughout the world from water depths of approximately 15–50 m (Thorson 1957; Buchanan 1957; Dörjes 1971; Wu and Richards 1981; Powell 1937). Aporrhaid gastropods today have a fairly restricted geographical distribution, but are found abundantly with *Turritella* in the Irish Sea (Jones 1956), off the Atlantic Coast of Spain (Cadée 1968), the Mediterranean (Thorson 1957), and off the eastern coast of the U.S.A. (Perron 1978). Such *Aporrhais* and *Turritella* dominated communities often grade laterally into the so-called '*Venus*' communities which contain abundant venerid bivalves, *Corbula*, *Spisula*, *Tellina*, and naticid gastropods (Thorson 1957).

The 'oceanic zone' community developed on sand at 40–85 m off the Atlantic coast of Spain (Cadée 1968) has abundant *Turritella* and *Aporrhais* together with *Natica*, several predatory neogastropods, as well as abundant *Glycymeris*, species of Cardiidae, Veneridae, Tellinidae, and *Corbula*. This fauna seems to be very similar in character to that of the Blackdown Greensand. Trigonid bivalves are, of course, absent from these modern communities, but species of their probable ecological equivalents, the Cardiidae, are frequently abundant.

## THE GASTROPODS AND THEIR TROPHIC POSITION

The Blackdown Greensand gastropod fauna comprises at least sixty-five species, including fifty-seven proso-branchs and eight opisthobranchs (Table 1 and Appendix 2). It was considered necessary to provide systematic descriptions for the predators referred to in this study and the authors have published their revised nomenclature elsewhere (Morris and Cleevely, in press). Authorities for species may be found in the Appendix.

The most abundant gastropod family is the Aporrhaidae, which comprise 34% of the total gastropod numbers (text-fig. 1). Nine species have been recorded but only three of these, namely; *Perissoptera parkinsoni* (83 individuals); *Drepanocheilus neglecta* (275); and *D. calcarata* (956), are common. A similar abundance and diversity of aporrhaids occurs in other marine Albian deposits of north-west Europe. Both *D. neglecta* and *D. calcarata* appear to be endemic to the Blackdown facies although closely similar species are found elsewhere. Living aporrhaids feed upon epilithic algae, diatoms, and detritus (Perron 1978).

The Turritellidae, particularly *Turritella granulata* are the next most abundant gastropod group, comprising 18% of individuals. Living *Turritella* are shallow-burrowing ciliary suspension feeders (Fretter and Graham 1962). Other herbivorous groups represented are the Trochacea, Cerithiacea, Rissoacea, and Littorinacea (Fretter and Graham 1962; Houbrick 1974, 1978).

TABLE 1

*a.* Ranked abundance of gastropods in the Blackdown Greensand
fauna by family or superfamily

|  | Individuals | Species |
|---|---|---|
| 1. Aporrhaidae | 1,325 | 9 |
| 2. Turritellidae | 706 | 2 |
| 3. Acteonidae | 497 | 4 |
| 4. '*Murex*' *calcar* | 380 | 1 |
| 5. Naticacea | 302 | 4 |
| 6. Cerithiacea | 174 | 13 |
| 7. Muricacea (*sensu* Ponder 1973) | 145 | 12 |
| 8. Littorinacea | 124 | 1 |
| 9. Ringiculidae | 79 | 1 |
| 10. Trochacea | 75 | 4 |
| 11. Epitoniidae | 35 | 3 |
| 12. Pyramidellidae | 24 | 2 |
| 13. Rissoacea | 13 | 4 |
| 14. Fossaridae | 9 | 2 |
| 15. Vanikoridae | 3 | 1 |
| 16. Scaphandridae | 2 | 1 |
| 17. Pleurotomariacea | 1 | 1 |
|  | 3,894 | 65 |

*b.* Ranked abundance of the most common gastropod species

| | |
|---|---|
| 1. *Drepanocheilus calcarata* | 956 |
| 2. *Turritella granulata* | 704 |
| 3. '*Murex*' *calcar* | 380 |
| 4. *Tornatellaea affinis* | 356 |
| 5. *Drepanocheilus neglecta* | 275 |
| 6. *Forator parkinsoni* | 189 |
| 7. '*Littorina*' *conica* | 124 |
| 8. *Cirsocerithium gracile* | 122 |

We are uncertain of the systematic position of another of the more common gastropods, '*Murex*' *calcar*. Although it possesses some morphological features in common with the Miocene to Recent genus *Murex sensu stricto*, we believe that these result from convergence. For the present paper, our conclusion is to consider '*M*.' *calcar* as belonging to an undescribed genus of the Mesogastropoda, that is perhaps related to the Strombacea.

There are three species of Epitoniidae in the fauna; all living members of this family are carnivorous, feeding upon various soft-bodied or skeletalized anthozoans (Robertson 1970, 1980).

Four species, comprising 302 individuals, can be referred to the Naticacea (text-fig. 2); in order of abundance these are: *Forator parkinsoni* (63%); *Pictavia rotundata* (25%); *Gyrodes gentii* (9%); and *G. dupinii* (3%). Living naticaceans are active predators feeding by shell drilling, largely upon molluscan prey (Ziegelmeier 1954; Edwards 1974). Naticacean gastropods are known from the lower Jurassic, but drill holes that can confidently be attributed to their activities are not recognized in any abundance before the Albian (Sohl 1969). The inevitable conclusion is that pre-Albian Naticacea were not shell drillers. Three of the Blackdown naticids, *G. gentii*, *G. dupinii*, and *P. rotundata*, occur in other Albian and Aptian deposits, in which drill holes have not been found. *F. parkinsoni*, the most abundant naticid in the fauna, appears to be restricted to the Blackdown Greensand apart from a few small specimens in the Gault. This species is quite distinct in shell morphology from any earlier naticid taxa, and is the probable drilling predator amongst the Blackdown naticids. The other naticids are assumed to be carnivores and possibly, like some living naticids, they fed upon bivalves without the necessity
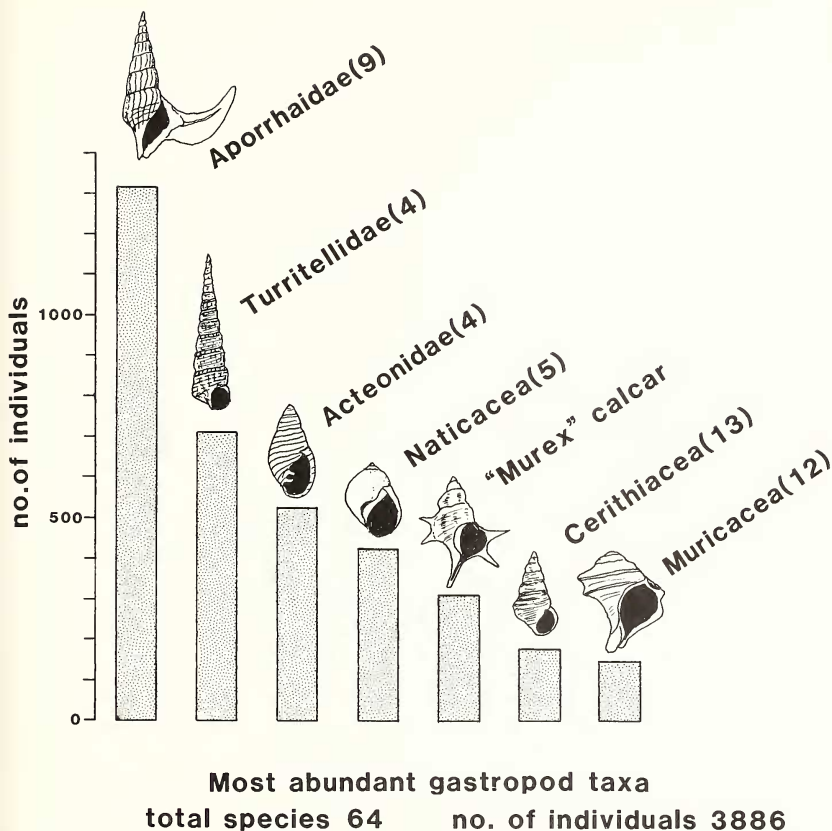
TEXT-FIG. 1. Relative abundance of the seven most common gastropod taxa in the Blackdown Greensand samples.

of drilling (Turner 1955; Vermeij 1980). Most pre-Albian naticids have been classified in the subfamily Ampullo-spirinae and Sohl (1969) considered that the first naticid drill holes coincide with the first appearance of members of the subfamily Polinicinae during the Albian. However, the assignment of Mesozoic naticids to one or other of the Recent families is a highly subjective exercise.

Twelve species of gastropods comprising only 4% of the total individuals may be referred to the order Neogastropoda. Most living taxa in this order are active carnivores and predators (Taylor *et al.* 1980); exceptions are a few species of Nassariidae and Columbellidae which are detritivores and herbivores. Although we are confident that these twelve are neogastropods, it is difficult solely on the basis of shell characters to refer
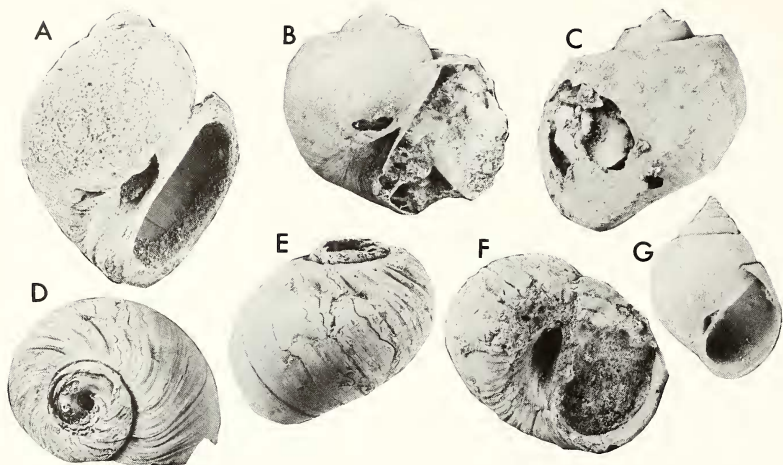
TEXT-FIG. 2. Naticacea from the Blackdown Greensand. A, *Forator parkinsoni* Morris and Cleevely, BM(NH) 57302, ×2. B, C, *Gyrodes gentii* (J. Sowerby), BM(NH) 34755, both approx. ×2. D, E, F, *Gyrodes dupinii* Deshayes and Leymerie, BM(NH) G 16112, ×3. G, *Pictavia rotundata* (J. Sowerby), BM(NH) G 16154, Vicary Colln, ×3.

them to higher taxa. Ponder (1973) provided the most recent review of relationships within the order and all of the Blackdown species apparently fall into his superfamily Muricacea; there are no examples of the Conacea and probably none of the Cancellariacea. The Muricacea (*sensu* Ponder) is a large taxon comprising most neogastropod families, but the relationships of the component families are at present obscure.

Amongst the twelve species (text-fig. 3) of neogastropods that we have recognized, five (comprising 54% of individuals) have shell characters that compare well with certain Muricidae, particularly those that have a less specialized shell form than either the Muricinae, or the Typhinae which we have not recognized before the Maastrichtian.

?*Paramorea lineata* is a small whelk-shaped species quite distinct from others in the fauna, it differs from *P. lirata* Wade (Campanian, U.S.A.) in lacking a ramp to the whorl and having a less truncated siphonal fasciole. Wenz (1938) placed the *Morea* group of genera in the Drupinae (= Thaidinae) and Stephenson (1941) introduced a family Moreidae (now Moreinae). *Morea* and *Paramorea* are similar in general shell form to species of present-day Thaidinae and although we have as yet no succession of these taxa through the Cretaceous–Tertiary boundary, we suspect that the Moreinae are early Thaidinae. The vast majority of living members of this family feed by drilling sedentary prey, e.g. other molluscs and barnacles, although a few species eat polychaetes, sipunculids, or corals (Taylor 1976, 1978).

Four other species occurring at Blackdown are somewhat similar to the living genus *Rapana*, considered to have a primitive shell form for the Muricidae, in having large equi-dimensional apertures and short upturned necks. *Semipirum depressum* has a large tangential aperture with virtually a flat spire that has a tendency towards a limpet-like form. There is a suggestive similarity to the Recent alcyonarian-feeding genus *Rapa*, but the limpet-like shape may be due to convergence, as occurs in the thaid limpet *Concholepas*. It is suspected that this shape is probably an adaptation for clinging to hard substrate. The similarity of ornament and whole shape to *Hillites downesi* and *Culmia brighti* are thought to be of more taxonomic significance and suggest that *S. depressum* may be a limpet-like early rapanid.

*H. downesi* has a distinct spire, a sharply incurved neck, and a relatively smaller tangential aperture. We agree

with Stephenson (1952, p. 181) that this genus may be related to *Sargana*, but find some difficulty in deciding whether the Sarganinae should be synonymized with the Rapaninae. *Sargana* has a more advanced aperture and delimited anterior canal than occurs in living *Rapana*, characters that resemble those of living Coralliophilidae. Although particularly concerned at the lack of *Rapana*-like taxa in the upper Cretaceous, we have tentatively included *Hillites* in the Rapanidae.

*C. brighti* has the generalized shell form of *Rapana* but with only fine spiral ornament. It is similar to *Ecphora* (?Cenoman.–Plio.) which suggests inclusion of *Culmia* in the Rapaninae.

*Blackdownia quadrata* has different shell ornament and apertural shape to *C. brighti*, and is a taller species. Although we follow Kollmann (1976, p. 196) and include this species in the Rapaninae, its form but not its ornament resembles *Forreria*, better placed in the Trophoninae, rather than *Rapana*. Shell shape also indicates some similarity to species of the genus *Pyropsis* (Cretaceous, see Sohl 1964, pl. 34) which have been placed in the Vasidae. Comparable intermediate vasids, with long and short siphonal canals, are still living (Abbott 1959), but their biology is not well known. Although Sohl may be correct in his assignment of *Pyropsis*, we consider that *Blackdownia* has a much more upwardly twisted shell neck than is found in that genus. Present-day Rapaninae feed by drilling both epifaunal and infaunal bivalves and live upon both sandy and rocky substrates (Gomoiu 1972).

Four of the Blackdown species can be confidently assigned to the family Fasciolariidae as currently recognized but which we consider to be paraphyletic.

*Resabulum rusticum* is a squat, rather whelk-shaped fasciolariid that closely resembles a number of north-west European Palaeocene species that have been wrongly attributed to *Siphonalia*, particularly '*Siphonalia*' *mariae* (Melleville) from the Thanet Sands, a similar facies to the Blackdown Greensand.

*Iscafusus rigidus* is one of the commoner species of neogastropods occurring in the Blackdown Greensand and is also relatively frequent in the Gault Clay facies at Folkestone. It is much taller than *R. rusticum* and has a form superficially similar to *Pleuroploca*, or *Palaeosephia*.

*Dumnonia collisnigrae* has a last whorl that is closely comparable to that of *I. rigidus*, but its earlier whorls are much more depressed and rounded. Finally, a fragment of '*Fusus*' *dubius* shows the tall turreted spire typical of the Fusininae.

Living species of Fasciolariidae feed upon polychaetes and molluscs; it is the larger forms such as *Pleuroploca* that feed upon molluscs (Paine 1966 and J. D. Taylor, pers. observation) whilst the smaller forms such as
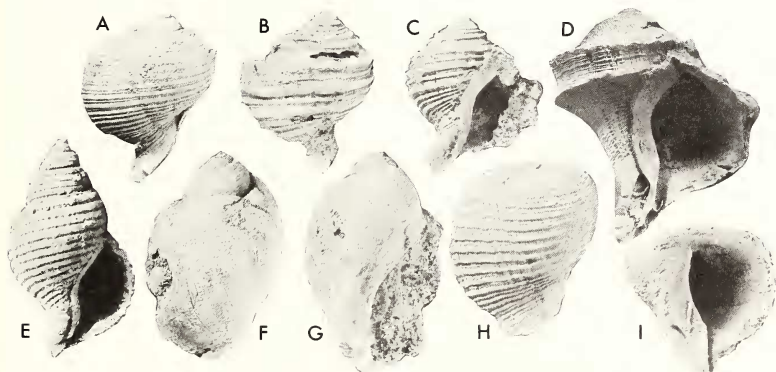


TEXT-FIG. 3*a*. Muricacea and possible Muricacea from the Blackdown Greensand. A, *Hillites downesi* Morris and Cleevely, Exeter Museum, Downes Colln, × 4. B, C, *Culmia brighti* (J. de C. Sowerby), Exeter Museum 97/1971, Downes Colln, × 2, from upper Greensand, Coombe Raleigh, nr. Honiton, Devon. D, *Blackdownia quadrata* (J. de C. Sowerby), BM(NH) G 16153, × 1·5. E, ?*Paramorea lineata* (J. de C. Sowerby), BM(NH) GG 20975, × 5. F, G, *Cosnia cosnensis* (de Loriol), Taunton Museum 7304, Fox Colln., × 3. H, I, *Sempirum depressum* (J. de C Sowerby), H, IGS 6851, × 3, I, Sedgwick Museum B 44819, × 3.
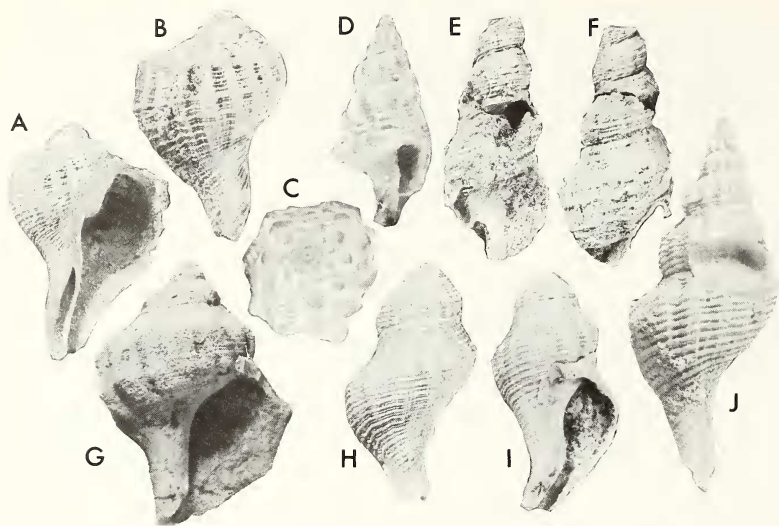
TEXT-FIG. 3*b*. Fasciolariidae, ?Melongeniidae, and ?Mitridae from the Blackdown Greensand. A, B, *Tantunia clathrata* (J. de C. Sowerby), BM(NH) 34838, A, × 3·5, B, × 3. C, D, ?Mitridae, BM(NH) GG 21286, Vicary Colln, C, × 10, apical view, D, × 8 (note the four plaits on the columella). E. F. ?Fasciolariidae, IGS 5763, × 2·5. G, *Resabulum rusticum* (J. de C. Sowerby), Bristol Museum Ca 5637, × 2. H, I, *Dumnonia collisnigrae* Morris and Cleevely, Taunton Museum 7502, × 2·5. J, *Iscafusus rigidus* (J. de C. Sowerby), Sedgwick Museum B 44899, × 3.

*Fusinus, Peristernia, Cantharus,* and *Leucozonia* mainly eat polychaetes, although they occasionally eat small gastropods (Taylor 1978 and unpublished records). As the Blackdown fasciolariids are all small they would be expected to have been polychaete feeders.

Each of the remaining three species have characters in common with different neogastropod families. One unnamed species (text-fig. 3) has a fasciolariid shell form, but three prominent columellar plaits suggest that it could have been an early mitrid. The mitrids may have been an early offshoot of the fasciolariid paraphyletic stem group. Most living Mitridae that have been studied feed upon sipunculid worms (Taylor *et al.* 1980).

*Cosnia cosnensis* has no columellar plaits but in other ways resembles the upper Cretaceous genera *Ptychoris, Ficulomorpha,* and *Palaeatractus,* all traditionally placed in the Volutidae, and *Mataxa* which Sohl (1964, p. 267) referred to the Cancellariidae. The Cenomanian genus *Carota* Stephenson (1952, p. 184) appears to be the earliest with the characteristics of the Volutidae and is quite different from this group of genera. Further, we remain unconvinced that they belong to the Cancellariacea. Consequently, we are uncertain as to their correct position. Present-day Volutidae mainly feed upon other Mollusca (Taylor *et al.* 1980).

*Tantunia clathrata* bears a superficial resemblance to the *Busycon* group, normally placed in the Melongenidae. If these similarities do not indicate a close relationship, they may at least indicate a comparable mode of life. Most living members of the Melongenidae feed upon other molluscs (Paine 1963; Hathaway and Woodburn 1961).

Shelled opisthobranchs are diverse and abundant in the Blackdown fauna, comprising 16% of the total gastropods (text-fig. 4). Four species can be referred to the family Acetonidae; one, *Avellana incrassata,* to the Ringiculidae; and one, *Cylichna,* to the Scaphandridae. The Acetonidae, with the two commonest species
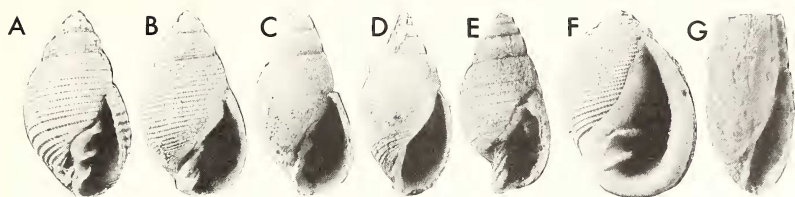
TEXT-FIG. 4. Opisthobranchs from the Blackdown Greensand. A, *Tornatellaea ebrayi* de Loriol, BM(NH) GG 20980, Vicary Colln, × 4. B, *Tornatellaea affinis* (J. de C. Sowerby), BM(NH) GG 20986, Vicary Colln, × 4. C, ?*Lacrimiformia pusilla* (J. de C. Sowerby), BM(NH) G 16110, Vicary Colln, × 4. D, *Tornatellaea* cf. *unisulcata* de Loriol, BM(NH) GG 20990, Vicary Colln, × 5. E, *Tornatellaea* cf. *cosnensis* de Loriol, BM(NH) GG 20989, Vicary Colln, × 5. F, *Avellana incrassata* (J. de C. Sowerby), BM(NH) G 704, Sir P. de Malpas Grey Egerton Colln, × 5. G, *Cylichna* sp. cf. *urgonensis* Pictet and Campiche, Sedgwick Museum, Cambridge B 45015, × 10.

*Tornatellaea affinis* and *T. ebrayi*, form the largest single group of predatory gastropods in the Blackdown fauna. All living species of acteonid gastropods that have been studied feed upon polychaetes (Hurst 1965; Rudman 1972; Taylor, in prep.). The data are much less satisfactory for *Ringicula*, but a few gut samples (Pelseneer 1925; Fretter 1960) have recorded foraminifera and interstitial copepods. Study of various species of Scaphandridae, including *Cylichna*, indicates that they feed upon small bivalves, gastropods, foraminifera, and echinoderms (Thompson 1976).

Two species may be referred to the genus *Lacrimiformia* which Sohl (1964) has assigned to the Pyramidellidae. Many living species of this family are parasitic upon bivalves and polychaetes; a few of the larger species are apparently free-living in sandy substrates, but there are no details available of their diets.

In summary, by comparison with living gastropods, the most abundant trophic category in the Blackdown Greensand (Table 2) is the detritivores and algal feeders (44% of individuals), followed by predators and carnivores (28%), and suspension feeders (18%). By far the most abundant trophic group of the carnivores is that of the polychaete feeders, which comprises over half (51%), with that of the mollusc feeders forming 25% and

TABLE 2. Presumed diets of Blackdown Greensand gastropods (see text for details)

*a.* Trophic classification of the Blackdown Greensand gastropod fauna

|  | Individuals | Per cent |
|---|---|---|
| Algal feeders and detritivores | 1,715 | 44 |
| Suspension feeders | 706 | 18 |
| Carnivores and predators | 1,086 | 28 |
| Unknown ('*Murex*' calcar) | 380 | 10 |

*b.* Possible diets of the carnivorous and predatory gastropods

|  | Individuals | Per cent |
|---|---|---|
| Polychaete feeders (Acteonidae and Fasciolariidae) | 554 | 51 |
| Drilling of molluscs (Naticacea and Muricidae) | 268 | 25 |
| Mollusc feeding (*Tantunia* and *Cylichna*) | 8 | 1 |
| Anthozoans (Epitoniidae) | 35 | 3 |
| Microzoobenthos (Ringiculidae) | 79 | 7 |
| Parasitic ? (*Lacrimiformia*) | 24 | 2 |
| Unassigned (non-drilling naticids and other gastropods) | 118 | 11 |

feeders upon the microbenthos amounting to 7%. The percentage of the fauna that we could not assign (11%) includes the non-drilling naticaceans and a few neogastropods.

The sandy fauna occurring in the Blackdown Greensand is similar in composition to other Albian sandy faunas known from north-west Europe (Marlière 1939; de Loriol 1882); there are also diverse marine mud faunas of similar age, which have particular elements in common. In present-day, sublittoral sandy benthic communities, polychaetes are usually the most abundant macro-invertebrate group and in the few soft-substrate gastropod assemblages that have been studied, polychaete feeders form the major trophic category (Taylor, in press).

## DRILLING PREDATION

Predation holes made by gastropods can be distinguished from holes in shells by other predatory and non-predatory organisms (see cautionary review by Bromley 1981). Examples of the holes made by living naticid and muricid gastropods were used as the basis for the recognition of predation in the Albian specimens. Any doubtful holes were rejected from the analysis. It is probable that a proportion of these holes were authentic gastropod drills, but altered by taphonomic processes and therefore to a small degree we have underestimated predation rates.

The living nudibranch *Okadaia elegans* from the western Pacific can make drill holes resembling those of *Natica* in small polychaete tubes (Young 1968; figure in Kay 1979) and Bromley (1981) raised the possibility that nudibranchs existing in the past, but which have left no trace of their occurrence, may have caused some of the drill holes in fossil molluscs. This, of course, is feasible, but *Okadaia* is very small (0·6–4·0 mm), the holes it produces are very small, and it is the only nudibranch known both feeding on polychaetes and having a drilling habit (Todd 1981). Additionally, no nudibranchs are known that feed upon shelled molluscs. The existence of Albian nudibranchs is not testable, but this possibility has to be kept in mind. Opisthobranchs with reduced shells that may be nudibranch precursors are, however, not known before the lower Cainozoic (Zilch 1959).

Secondly, a distinction must be made between the holes made by naticid and muricid gastropods. The features of the drilled holes produced by the two families have been extensively documented and illustrated (Fretter and Graham 1962; Carriker and Yochelson 1968; Sohl 1969; Fischer 1922; Hoffman *et al.* 1974; Robba and Ostinelli 1975; Ziegelmeier 1954; Carriker and van Zandt, 1972; Bromley 1981). Typically, naticid holes are wide exteriorly and narrow internally with a countersunk rim ('truncated paraboloid' of some authors); muricid holes are, by contrast, straight-sided, slightly conical or cylindrical in form. However, in both these gastropod families the shape of the hole they produce may vary considerably with different prey, or its position on the shell. In certain cases the identification of the shell driller may not be possible. Naticid drillings, for instance, into the bivalve *Corbula* tend to be nearly cylindrical, but broad in the outer shell layer and somewhat narrower through the inner layer, thereby producing a stepped appearance (Ziegelmeier 1954). Such borings can resemble those made by muricids as Hoffman *et al.* (1974) noted, and in some earlier studies (Taylor 1970; Kojumdjieva 1974) these borings have been wrongly assigned.

It must be borne in mind that a proportion of prey eaten by naticids and muricids need not be drilled. Naticids are known to eat *Ensis* and small Tellinidae without drilling (Turner 1955; Vermeij 1980), and some muricids eat gastropods through the aperture, or in the case of limpets by prising them off the rocks (Taylor 1976), or bivalves by inserting their proboscis between the valves (Broom 1982).

Lever and Thijssen (1968) have shown that drilled and undrilled shells differ in their hydrodynamic properties and post-mortem transportability. However, their studies were carried out on intertidal sandy beaches, where shell transport can be considerable, but in sublittoral habitats such transport is usually greatly reduced (Warme 1969; Ekdale 1977). In the Blackdown Greensand habitat, we have assumed that drilled and undrilled shells had the same probability of preservation.

*Predation upon bivalves*

Eighty-three species from twenty-three superfamilies, comprising some 6,885 valves, representing 3,442 individual bivalves, were recorded in our examination of the Blackdown Greensand fauna. Thirty-six of these species are uncommon and only represented by ten, or fewer, valves. Table 3 shows the ranked abundance of the various families (3*a*); and the ten most abundant species of bivalve in the fauna (3*b*; see also text-fig. 5).
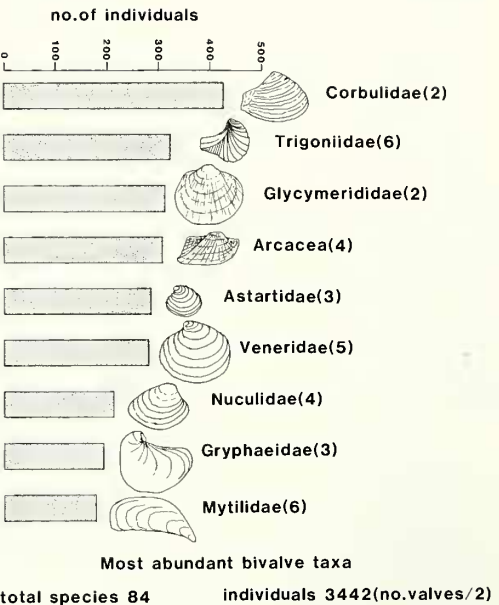
The two commonest species *Corbula elegans* and *Nicaniella formosa* are both small molluscs (4·8 mm and 3·6 mm respectively). Most of the bivalves in the fauna are shallow-burrowing in habit and these comprise 79% of individuals, with species in the Glycymeridicae, Trigoniidae, Veneracea, Corbulidae, and Arcticidae as the dominant elements (Table 3). Thinner-shelled, deeper burrowers from the Tellinacea, Solenacea, and Pholadomyacea form a mere 2% of the total individuals, but it is likely that members of this group are less well preserved and under-represented in collections.

TABLE 3

*a.* Ranked abundance and diversity of bivalves in the Blackdown Greensand fauna by family or superfamily

|  | Valves | Species |
|---|---|---|
| 1. Corbulidae | 857 | 2 |
| 2. Trigoniidae | 646 | 6 |
| 3. Glycymerididae | 627 | 2 |
| 4. Arcacea | 620 | 4 |
| 5. Astartidae | 571 | 3 |
| 6. Veneracea | 559 | 5 |
| 7. Nuculacea | 414 | 4 |
| 8. Gryphaeidae | 386 | 2 |
| 9. Mytilacea | 353 | 6 |
| 10. Cardiacea | 335 | 6 |
| 11. Arcticidae | 325 | 4 |
| 12. Tellinacea | 253 | 5 |
| 13. Pteriacea | 229 | 7 |
| 14. Nuculanacea | 220 | 2 |
| 15. Mactracea | 158 | 2 |
| 16. Pectinacea | 118 | 7 |
| 17. Lucinacea | 97 | 4 |
| 18. Poromyacea | 57 | 1 |
| 19. Pholadomyacea | 39 | 3 |
| 20. Limacea | 10 | 4 |
| 21. Pinnacea | 6 | 1 |
| 22. Thraciacea | 4 | 2 |
| 23. Solenacea | 1 | 1 |

*b.* Ranked abundance of the most common bivalve species

|  | Valves |
|---|---|
| 1. *Corbula elegans* | 712 |
| 2. *Nicaniella formosa* | 552 |
| 3. *Glycymerita umbonata* | 425 |
| 4. *Idonearca glabra* | 395 |
| 5. *Amphidonte obliquata* | 375 |
| 6. *Nucula antiquata* | 224 |
| 7. *Nanonavis carinatus* | 220 |
| 8. *Glycymerita sublaevis* | 202 |
| 9. *Callistina plana* | 201 |
| 10. *Protocardia hillana* | 200 |

TABLE 4. Frequency of drilling by naticid and muricid gastropods upon bivalves. Only the most commonly attacked species are listed here (complete data in Appendix 1)

| Species | No. of drills | Per cent of total drilling | No. of naticid drills | Per cent of naticid drills | No. of muricid drills | Per cent of muricid drills |
|---|---|---|---|---|---|---|
| *Corbula elegans* | 42 | 18 | 42 | 28 | — | — |
| *Amphidonte obliquata* | 31 | 13 | 3 | 2 | 28 | 33 |
| *Glycymerita umbonata* | 26 | 11 | 15 | 10 | 11 | 13 |
| *Nicaniella formosa* | 16 | 7 | 15 | 10 | 1 | — |
| *Idonearca glabra* | 12 | 5 | 7 | 5 | 6 | 6 |
| *Protocardia liliana* | 9 | 4 | 7 | 4 | 3 | 4 |
| *Palaeomoera inaequalis* | 9 | 4 | 9 | 6 | — | — |
| *Glycymerita sublaevis* | 7 | 3 | 2 | 1 | 5 | 6 |
| *Epicyprina angulata* | 7 | 3 | 4 | 3 | 4 | 4 |
| *Modiolus reversa* | 7 | 3 | 4 | 3 | 3 | 3 |
| *Corbula truncata* | 7 | 3 | 7 | 5 | — | — |
| *Chinela caperata* | 4 | 2 | 4 | 3 | — | — |
| *Nucula antiquata* | 4 | 2 | 4 | 3 | — | — |
| *Falcimytilus lanceolatus* | 5 | 2 | — | — | 5 | 6 |
| *Nanonavis carinatus* | 4 | 2 | — | — | 4 | 5 |
| Total drills all species | 241 | | 152 | | 89 | |
| Total species drilled | 43 | | 32 | | 24 | |



TEXT-FIG. 5. Relative abundance of the nine most common bivalve families in the Blackdown Greensand fauna.

no. of individuals

Corbulidae (2)
Trigoniidae (6)
Glycymerididae (2)
Arcacea (4)
Astartidae (3)
Veneridae (5)
Nuculidae (4)
Gryphaeidae (3)
Mytilidae (6)

Most abundant bivalve taxa

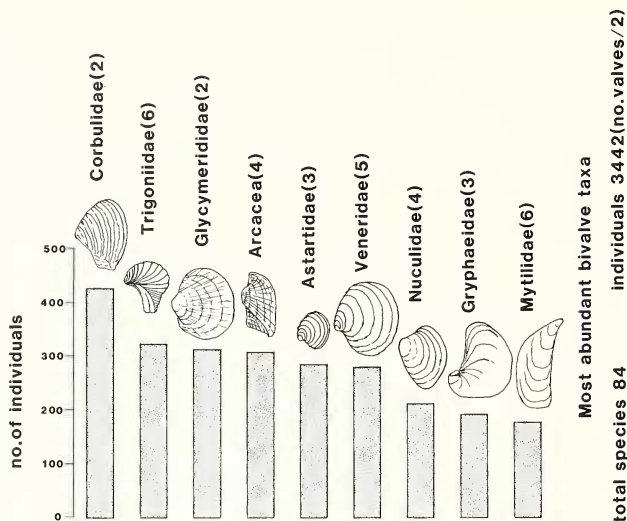total species 84        individuals 3442 (no. valves/2)

TEXT-FIG. 5. Relative abundance of the nine most common bivalve families in the
Blackdown Greensand fauna.

TABLE 4. Frequency of drilling by naticid and muricid gastropods upon bivalves. Only the most commonly
attacked species are listed here (complete data in Appendix 1)

| Species | No. of drills | Per cent of total drilling | No. of naticid drills | Per cent of naticid drills | No. of muricid drills | Per cent of muricid drills |
|---|---|---|---|---|---|---|
| *Corbula elegans* | 42 | 18 | 42 | 28 | — | — |
| *Amphidonte obliquata* | 31 | 13 | 3 | 2 | 28 | 33 |
| *Glycymerita umbonata* | 26 | 11 | 15 | 10 | 11 | 13 |
| *Nicaniella formosa* | 16 | 7 | 15 | 10 | 1 | 1 |
| *Idonearca glabra* | 12 | 5 | 7 | 5 | 5 | 6 |
| *Protocardia hillana* | 9 | 4 | 6 | 4 | 3 | 4 |
| *Palaeomoera inaequalis* | 9 | 4 | 9 | 6 | — | — |
| *Glycymerita sublaevis* | 7 | 3 | 2 | 1 | 5 | 6 |
| *Epicyprina angulata* | 7 | 3 | 4 | 3 | 3 | 4 |
| *Modiolus reversa* | 7 | 3 | 4 | 3 | 3 | 4 |
| *Corbula truncata* | 7 | 3 | 7 | 5 | — | — |
| *Chimela caperata* | 4 | 2 | 4 | 3 | — | — |
| *Nucula antiquata* | 4 | 2 | 4 | 3 | — | — |
| *Falcimytilus lanceolatus* | 5 | 2 | — | — | 5 | 6 |
| *Nanonavis carinatus* | 4 | 2 | — | — | 4 | 5 |
| Total drills all species | 241 | | 152 | | 89 | |
| Total species drilled | 43 | | 32 | | 24 | |

Epifaunal and endobyssate bivalves comprise 19% of individuals, most common being the exogyrid oyster *Amphidonte obliquata*, the byssate arcid *Nanonavis carinatus*, mytilids, and inoceramids.

Forty-three species of bivalve are eaten by predatory gastropods, but 73% of attacks are made on eleven species (see Table 4 and Appendix 1). Eleven of these species are eaten exclusively by muricid gastropods, a further nineteen exclusively by naticids, and the remaining thirteen are eaten by both predators.

The most frequent prey drilled by muricid gastropods is the oyster *A. obliquata*, which amounts to 33% of muricid attacks, and this is followed by *Glycymerita umbonata* that has suffered 13%. As might be expected the prey of the muricids mainly consists of epifaunal and some shallow-burrowing species, which require little excavation from the substrate. Although some twenty-four species of bivalve are drilled by muricids, 69% of these attacks are made on only six species with 46% occurring on just two species.

The principal species of bivalve drilled by naticid gastropods is the small *C. elegans* which forms 28% of attacks, with *G. umbonata* and *Nicaniella formosa* each undergoing 10% of attacks. A total of thirty-two species are drilled by naticids, but 77% of all their predation occurs upon eleven species, all of which were probably burrowers, except for *Modiola reversa* that is thought to have been endobyssate, and a few drills occurring in the epifaunal *Amphidonte*.

Some prey are drilled by both naticid and muricid gastropods. The most notable of these are *G. umbonata*, *Protocardia hillana*, *Epicyprina angulata*, and *M. reversa*. The majority of these shared prey species are very shallow burrowers, or else endobyssate in habit and therefore available to both predators. A few naticid holes were observed in the lower cemented valve of *A. obliquata*; this small oyster lived attached to shell fragments on the sandy substrate and may have been occasionally taken in a manner similar to the irregular predation of the Recent *Polinices duplicatus* upon the epifaunal byssate *Mytilus edulis* (Edwards 1974).

*Predation upon gastropods*

We have recorded some 3,894 gastropod specimens representing the occurrence of sixty-five species in the Blackdown fauna (Table 1 and Appendix 2). The great majority of these species are uncommon and, in fact, five species account for 69% of the total individuals. By comparison with their living relatives, most of these more abundant species are considered to be shallow burrowers, or surface ploughers on soft substrates.

Twenty-three species of gastropods are drilled by naticids and four by muricids, with all of that four being drilled by both predators. The naticids are responsible for most of the predation upon gastropods (92%) with that by the muricids amounting to the remaining 8%. The ranked total predation by species is shown in Table 5 with the four species *Drepanocheilus calcarata*, *D. neglecta*, '*Murex*' *calcar*, and *Turritella granulata* suffering 74% of the attacks made by both of these predators. The same four prey species form 75% of naticid predation and also the greater part of that by the muricids.

*Prey preferences*

Kitchell *et al*. (1981) have recently provided a model for prey selection by naticid gastropods based upon a cost–benefit analysis of the different prey types. Although this approach, which they have applied to an analysis of predation by naticids on Miocene *Glycymeris*, is of considerable interest, we do not consider that the method is appropriate for the Blackdown Greensand fauna. The reasons for this are first, the low predation rate, and secondly, our lack of precise knowledge as to the natural abundance of the prey species. However, bearing in mind the limitations of the samples used in our own study, we can make some simple analyses of prey preferences.

If we compare predation rate against the relative abundance of bivalve families (text-fig. 6), then there is a significant (2% level) positive correlation with increasing abundance, reaching a peak in the Corbulidae. Conspicuous exceptions of this trend are found in the Gryphaeidae, which are drilled at a higher rate than their abundance would suggest, and in the Trigoniidae which are ranked second

TABLE 5. Gastropod species most commonly drilled by predatory gastropods. Complete data in Appendix 2

| Species | Total drilling | Per cent | Naticid drilling | Per cent | Muricid drilling | Per cent |
|---------|----------------|----------|------------------|----------|------------------|----------|
| *Drepanocheilus calcarata* | 49 | 23 | 43 | 22 | 7 | 44 |
| *D. neglecta* | 50 | 24 | 46 | 24 | 3 | 19 |
| '*Murex*' *calcar* | 37 | 18 | 32 | 16 | 5 | 31 |
| *Turritella granulata* | 26 | 12 | 26 | 13 | — | — |
| '*Littorina*' *conica* | 8 | 4 | 8 | 4 | — | — |
| *Tornatellaea affinis* | 7 | 3 | 7 | 4 | — | — |
| *Margarites monilifera* | 5 | 2 | 5 | 3 | — | — |
| *Avellana incrassata* | 4 | 2 | 4 | 2 | — | — |
| *Forator parkinsoni* | 4 | 2 | 4 | 2 | — | — |
| *Confusiscala fittoni* | 3 | 1 | 3 | 2 | — | — |
| *Gyrodes gentii* | 2 | 1 | 2 | 1 | — | — |
| *Pictavia rotundata* | 2 | 1 | 2 | 1 | — | — |
| *Tornatellaea* cf. *cosnensis* | 2 | 1 | 2 | 1 | — | — |
| *Blackdownia quadrata* | 2 | 1 | 2 | 1 | — | — |
| Total individuals drilled | 211 | | 195 | | 16 | |
| Total species drilled | 23 | | 23 | | 4 | |
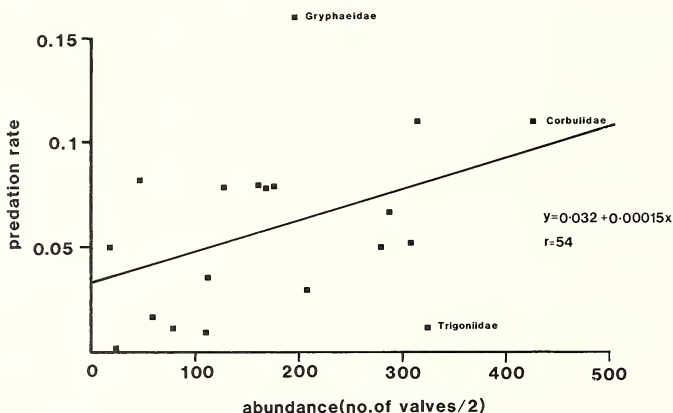


TEXT-FIG. 6. Relation of predation rate and family abundance for bivalves in the Blackdown Greensand fauna (Gryphaeidae and Trigoniidae excluded from regression analysis for reasons given in text).

in abundance, but have a very low predation rate. The explanation for this would seem to be that five of the six species of Trigoniidae in this fauna are thick-shelled and have a highly rugose shell ornament; they were also probably capable of a leaping movement in order to avoid predation as has been described by Stanley (1977a) for their living relatives. The oyster *Amphidonte* is the only really common epifaunal bivalve available to the muricids and it would have ranked first in accessibility to
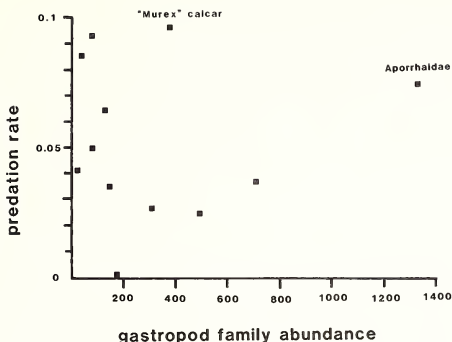
TEXT-FIG. 7. Relation of predation rate and family abundance
for gastropods in the Blackdown Greensand fauna.

them. Moreover, comparison with present-day oysters would suggest that the Albian oysters were locally aggregated, thereby increasing their local abundance.

For the gastropods (text-fig. 7) high predation rates are found amongst some of the least abundant families. Out of the more numerous taxa, '*M*.' *calcar* has the highest predation rate followed by the Aporrhaidae. Of the latter family *D. calcarata* is three times more abundant in our samples than is *D. neglecta*, but it has a predation rate of 5·1% which is significantly lower (chi square $p < 0·001$) than that of *D. neglecta* (18·2%). This indicates that if the relative abundance in our samples reflects the natural (living) frequency of the two species, then *D. neglecta* is being actively selected by the predators.

Perron (1978) has reported a marked seasonal change in the behaviour of living *Aporrhais occidentalis* (which probably also occurs in *A. pespelecani*), that would affect their availability to predators. The gastropods remain burrowed and quiescent from August until February but active on the sediment surface from February to late summer—although there is some variation in the length of this active period dependent upon sex and maturity. Such behavioural characteristics ought to be borne in mind when interpreting results obtained from fossil assemblages.

Our results tentatively suggest that the predators are tending to select the most abundant bivalve families, but avoiding the Trigoniidae. They also seem to be preferentially selecting the gastropods '*M*.' *calcar* and *D. neglecta*. It must be stressed that these data are based upon abundance in museum collections.

*Size of prey*

Living naticid gastropods show strong size selection of prey (Ansell and Mace 1978*a*; Kitchell *et al.* 1981), but we were unable to detect such behaviour in our admittedly small samples.

The size frequency distribution of the bivalves occurring in the Blackdown fauna is shown in text-fig. 8. The majority of the bivalves in the various assemblages (72%) are between 4 and 30 mm in length. The preponderance of small individuals is largely due to the great abundance of *C. elegans* and *N. formosa*. The sizes of the bivalves drilled show a very similar size distribution, with 79% of the individuals taken being between 4 and 30 mm. There was no significance difference (chi squared) between the sizes of the populations. For the most frequently drilled species, *G. umbonata*, *Amphidonte obliquata*, and *C. elegans*, there were similarly no significant differences (*t* test) between the sizes of drilled and undrilled shells.
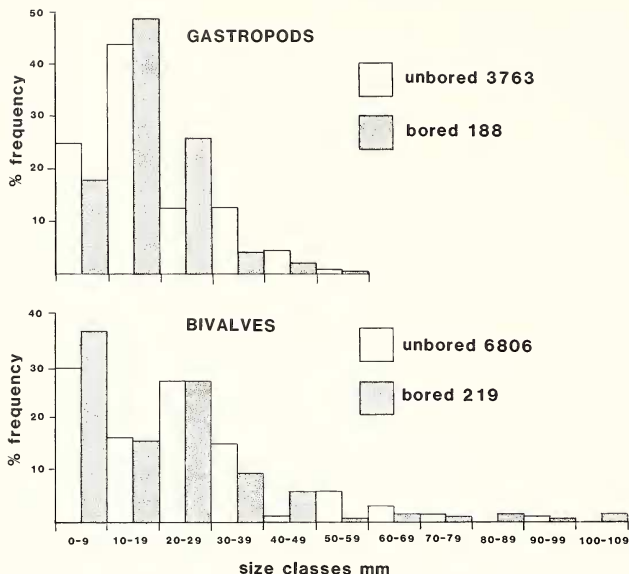
TEXT-FIG. 8. Comparison of the size frequency distributions of drilled and undrilled molluscs in the Blackdown Greensand fauna.

Taking the bivalve assemblage as a whole, the muricids drill significantly larger (t test $p < 0.001$) bivalves (mean shell length $= 29.5 \pm 18.2$ mm, $n = 75$) than naticids ($= 17.3 \pm 18.5$, $n = 144$). In the case of *G. umbonata* which was attacked by both naticid and muricid predators, those eaten by muricids (shell length $= 22.3 \pm 6.6$ mm, $n = 7$) were not significantly larger than those taken by naticids ($16.9 \pm 4.9$ mm, $n = 15$).

For gastropods the majority of the individuals (80%) are in the category of 3–30 mm in shell height and the drilled shells follow the same distribution (see text-fig. 8). Comparison of the two predominant aporrhaid species (text-fig. 9) reveals that *D. neglecta* (shell height $= 15.4 \pm 2.9$ mm, $n = 136$) is considerably larger (t test, $p < 0.001$) than *D. calcarata* (ht. $= 11.5 \pm 2.2$ mm, $n = 166$). There are no significant differences for either species in the sizes of drilled and undrilled shells. However, the drilled shells of *D. neglecta* ($15.6 \pm 1.82$ mm, $n = 36$) are significantly larger than those of *D. calcarata* ($10.5 \pm 1.95$ mm, $n = 42$). The much larger aporrhaid *Perissoptera parkinsoni* (mean shell height $= 37.9$ mm) is not drilled by either naticids or muricids.

*Drilling behaviour*

The siting of drill holes in the shell may illustrate aspects of the behaviour of the predator. This evidence cannot be used to distinguish between the activities of different species of naticids, for studies of living naticids have shown that the position drilled is dependent upon the size, shape, ornamentation, and behaviour of particular prey species; which are all factors that determine how the
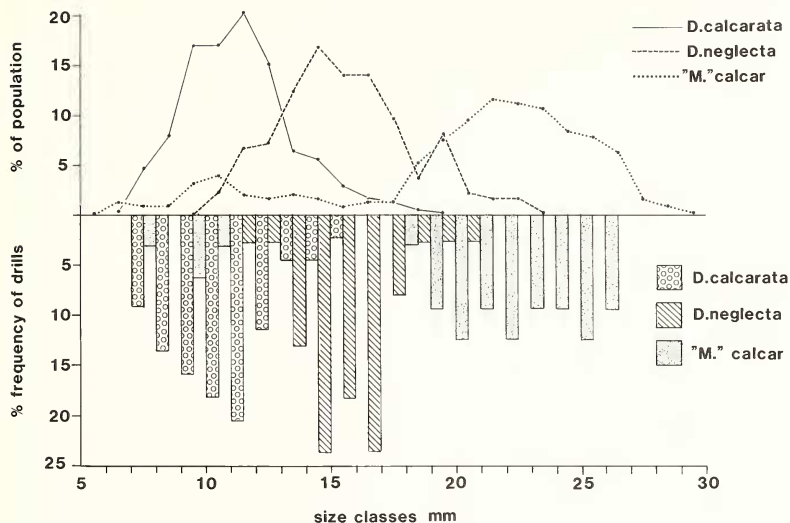
TEXT-FIG. 9. Size frequency distribution of drilled and undrilled shells for the three most heavily predated gastropod species, *Drepanocheilus calcarata*, *D. neglecta*, and '*Murex*' *calcar*.
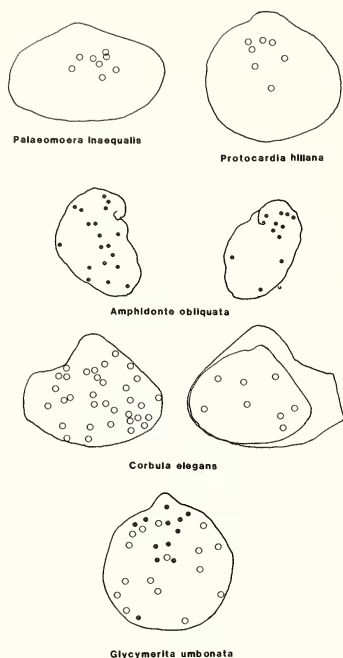
prey will be manipulated in the foot of the predator (Ansell 1960). Nevertheless, some living naticids do have a distinctive drilling style; for instance, *Polinices tumidus* usually drills bivalves across the valve margins at the ventral commissure (Vermeij 1980).

In *C. elegans* (text-fig. 10) where the two valves differ considerably in size, there are significantly more naticid holes (50% probability test $p < 0.002$; $n = 36$) in the larger right valve, which is the lower valve in life orientation, than in the smaller left valve ($n = 8$). Such a valve preference is not found in any of the other bivalve prey species, even in the oyster *Amphidonte* where the valves differ considerably in size.

In some prey species naticid drills are frequently consistently placed, e.g. in *Palaeomoera* and *Protocardia* (text-fig. 10), indicating similar handling and orientation in the foot prior to drilling. This stereotypy of drilling behaviour (Berg and Nishenko 1975) is usually seen on the shells of burrowing bivalves. In very shallow, or small bivalves such as *Glycymerita* and *Corbula* the position of the drill hole is more variable.

Muricid gastropods do not usually manipulate the prey with the foot, as naticids do, and the drill holes they produce tend to be more randomly positioned (Carriker and van Zandt 1972), which is exemplified by the muricid predation found in *Amphidonte* (text-fig. 10). Both naticids and muricids feed upon the surface burrower *G. umbonata*, but the muricid holes tend to be concentrated in the dorsal area of the shell, while the naticid holes are more widely dispersed. Glycymerid bivalves usually live in a near vertical, hinge-uppermost position, with the umbones at, or very near, the sediment surface (Thomas 1975). Since muricids have very limited powers for excavation of their prey, the dorsal areas of shells are the only sites available for them to drill. In contrast, naticids approach the prey within the sediment and then manipulate it in their foot.

Palaeomoera inaequalis

Protocardia hillana

Amphidonte obliquata

Corbula elegans

Glycymerita umbonata

TEXT-FIG. 10. Drill hole positions in four species of bivalves: open circles—naticid holes, solid circles—muricid holes.

Naticid drilling on gastropods also tends to be relatively stereotyped with each species tending to be drilled in a preferred position. The results of examination of the drill hole positions occurring in *D. calcarata* and *D. neglecta* are given in text-fig. 11. In both species significantly more (50% probability test) drills occurred upon the dorsal surface and although more attacks (23%) occurred on the ventral surface of *D. calcarata* compared with just 7% in *D. neglecta* this difference was not found to be significant (Yates's chi square). Most attacks on both species, whether dorsal or ventral, occurred in the second whorl (chi square $p < 0.01$). Division of the shell into three sectors (left side, central, and right side) showed that there was no significant preference for drill position between the three sectors.

Holes drilled across whorl boundaries were common in gastropods and examples of unproductive drilling into the apertural flange of aporrhaids, or occasionally the thicker varix area of other shells, were found. Instances of multiple drillings occurred; one *C. elegans* had six failed and one successful drill holes. Failed borings frequently occur in the Corbulidae (Fischer 1963; Hoffman *et al.* 1974; Ziegelmeier 1954). These failed drills often terminate at a unique organic periostracum-like layer situated between the outer and inner layers. This might be an adaptation to foil drilling predators. If so, then it was effective very early in the history of drilling predation upon the Corbulidae. A specimen of '*Fossarus*' *granosus* [Taunton Museum No. 6548] has one incomplete and five relatively complete holes, the majority of which show the typical naticid bevel. This probably indicates repeated
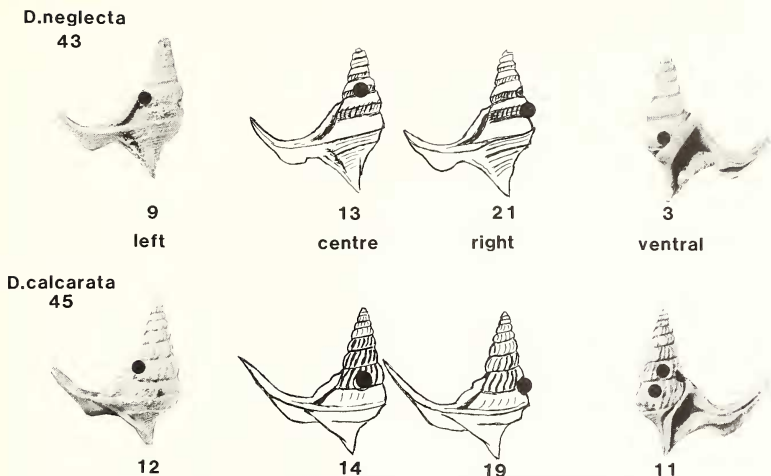
TEXT-FIG. 11. The positions and frequency of drills occurring in the two species of *Drepanocheilus*.

disturbance and dislodgement of the predator. Examples of multiple drillings arising from several individual predators drilling the same prey do not appear to occur for naticids, but are quite common with some muricids (Hughes 1980*b*; Taylor, pers. observation).

Some observations have related the size of the drill hole to the size of predator. However, for *Urosalpinx* (Muricidae), Carriker and van Zandt (1972) have shown that the diameter of the hole drilled by individual snails varied considerably according to their condition, their hunger state, and the degree of extension of the accessory boring organ. Another factor is that muricids do not need to manipulate their prey in the foot and can drill prey considerably larger than themselves.

The correlation of drill hole diameter and the size of the predator is more exact for naticids (Ansell and Mace 1978*a, b*; Wiltse 1980; Kitchell *et al.* 1981) although experimental observations have also indicated that both hunger state and radula wear (Ziegelmeyer 1954) influence matters. The diameter of the hole made by individual predators varies according to the nature of the prey species (Ansell and Mace 1978*a, b*). In the Blackdown fauna we have a wide variety of gastropod and bivalve prey eaten, but at low drilling frequencies. Consequently, it was decided that any general consideration of predator–prey size relationships would be pointless. Yet the relationship of drill hole diameter and prey size (shell height) in *Drepanocheilus* species was examined and we found that there was no correlation between the external diameter of the drill hole and prey size for either *D. calcarata* or *D. neglecta* (text-fig. 12), a result that was very different from the high correlation found for fossil *Glycymeris* by Kitchell *et al.* (1981).

*Summary of the diets of drilling gastropods in the Blackdown Greensand*

The main items in the diets of naticid and muricid gastropods, as deduced by the frequencies of drilled shells in the Blackdown Greensand, are shown in text-figs. 13 and 14.

The muricids drilled many more bivalves than gastropods (77%:23%) with oysters and shallow-burrowing bivalves comprising their main prey. Naticids drilled about the same number of
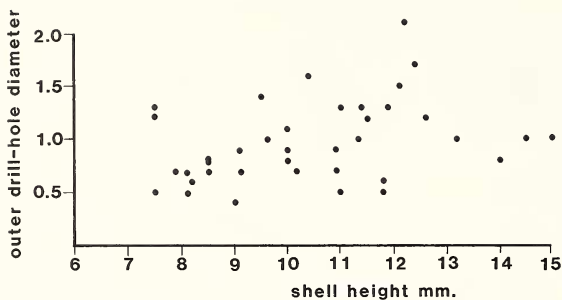
TEXT-FIG. 12. Plot of outer borehole diameter against prey height for *Drepano-cheilus calcarata*.
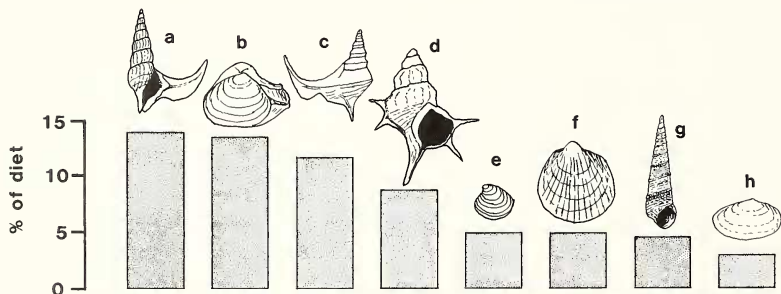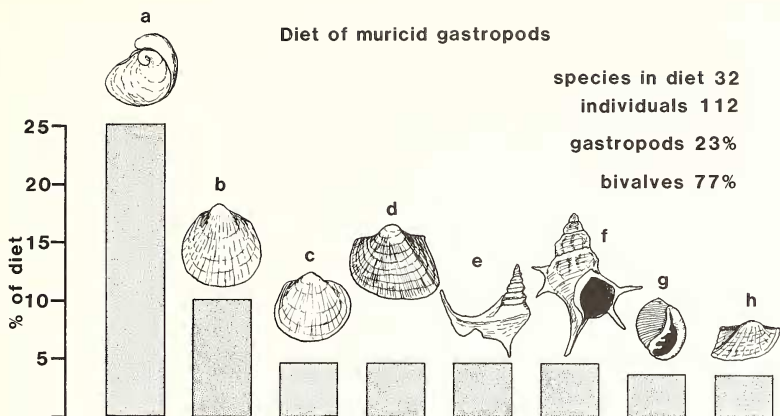


TEXT-FIG. 13. Percentage frequency of the eight most common prey items drilled by naticid gastropods. a, *Drepanocheilus calcarata*; b, *Corbula elegans*; c, *Drepanocheilus neglecta*; d, '*Murex*' *calcar*; e, *Nicaniella formosa*; f, *Glycymerita umbonata*; g, *Turritella granulata*; h, *Palaeomoera inaequalis*.

TEXT-FIG. 14. Percentage frequency of the eight most common prey items drilled by muricid gastropods. a, *Amphidonte obliquata*; b, *Glycymerita umbonata*; c, *Glycymerita sublaevis*; d, *Idonearca glabra*; e, *Drepanocheilus neglecta*; f, '*Murex*' *calcar*; g, *Avellana incrassata*; h, *Nanonavis carinatus*.

gastropods as bivalves (51%:49%), with their principal prey consisting of *Drepanocheilus* species, '*M.*' *calcar*, and *C. elegans*. The naticids also drilled a much greater number of prey species than muricids.

This relative balance in prey preference between gastropods and bivalves would appear to differ from the results of prey preference experiments on living *Polinices duplicatus* conducted by Wiltse (1980) and referred to by Kitchell *et al*. (1981, p. 535). In these, the preference ranking were found to be: *Mya* > *Mercenaria* > *Mytilus* > gastropods and these also coincided with what Kitchell *et al*. (1981) found to be the net profitability. Gastropods are also ranked low in the preference of the European *P. alderi* (Ansell, pers. comm.).

CONCLUSIONS

The Blackdown Greensand fauna is one of the most diverse and well-preserved Albian faunas—a time at which the major evolutionary radiation of predatory prosobranchs was beginning (Taylor *et al*. 1980). Despite the limitations imposed by the lack of current exposures, the Blackdown fauna, as recognized from museum collections, is of considerable importance in the context of this radiation, for not only are there a variety of predatory gastropods in the 'assemblage', but also associated evidence of their predatory activities. Some of the earliest muricid gastropods known to us occur in the fauna and these are accompanied by the evidence of typical muricid drill holes in the shells of molluscan prey. Similarly, the earliest drill holes known to us which can reasonably confidently be assigned to the Naticidae are found in this fauna. The results of our analyses show that, despite the fact that these are early records of predation, the prey preferences and drilling behaviour of the Albian predators are clearly very similar to those displayed by their present-day equivalents. We have no evidence to suggest that the Albian naticids and muricids were less efficient in prey capture than their modern counterparts, even though Stanton and Nelson (1980) have suggested that cannibalism and eating a wide range of prey types indicated inefficient feeding for their Eocene naticids.

TABLE 6. Percentage frequency of predation upon Turritellidae, Glycymeridae, Corbulidae, and for total gastropod and bivalve assemblages in various faunas from the Cretaceous to the Recent. Data in some cases are recalculated from the original

Key to symbols: a—Adegoke and Tevesz (1974), b—Dudley and Vermeij (1978), c—Fischer (1966), d—George (1965), e—Hoffman *et al.* (1974), f—Kojumdjieva (1974), g—Matsukuma (1977), h—Robba and Ostinelli (1975), i—Smith (1932), j—Taylor (1970), k—Thomas (1976), l—Vermeij (1980).

| | Turritellidae | Glycymeridae | Corbulidae | All gastropods | All bivalves | Reference |
|---|---|---|---|---|---|---|
| **Cretaceous** | | | | | | |
| Albian, England | 4 | 10 | 11 | 5 | 4 | herein |
| Campanian, U.S.A. | 4 | | | | | b |
| **Eocene** | | | | | | |
| Paris Basin | 21 | 10 | 28 | 17 | 26 | j |
| Paris Basin | 63 | 9 | 22 | 26 | 13 | c |
| Nigeria | 30 | | 25 | 19 | 5 | a |
| **Miocene** | | | | | | |
| Poland | 19 | 40 | 27 | 11 | 14 | e |
| Bulgaria | 40*, 41* | 11 | 11 | | | f |
| Eastern U.S.A. | | 27 | | | | k |
| Eastern U.S.A. | 28 | | | | | b |
| **Pliocene** | | | | | | |
| Italy | 19 | | 16 | 14 | 15 | h |
| Eastern U.S.A. | | 24 | | | | b |
| **Recent** | | | | | | |
| Guam | | | | | 19 | l |
| Plymouth | | 23 | | | 24 | i |
| Japan | | 51, 73 | | | | g |
| Italy | | 34 | | | | d |
| Tropical (mean) | 32 | | | | | b |
| Temperate (mean) | 11 | | | | | b |

\* The two largest *Turritella* samples documented by Kojumdjieva (1974).

Glycymerid and corbulid bivalves, ·oysters, and *Turritella* are still, and were throughout the Cenozoic, important prey items of both the naticids and muricids (Ziegelmeier 1954; Hoffmann *et al.* 1974; Fischer 1966; Thomas 1976; Robba and Ostinelli 1975). Aporrhaid gastropods are one of the main items in the diet of the Albian naticids, but today that family is restricted to just two species in the Mediterranean and north-west Europe and one along the eastern coast of the U.S.A. To our knowledge there has not been a study of naticid predation upon these species, although examples of *Natica*-drilled specimens of *Aporrhais* occur in museum collections.

It has been suggested that there was a major increase in predation intensity during the late Mesozoic, which had profound effects upon the evolution of benthic invertebrates (Vermeij 1977). Drill holes produced by predatory gastropods afford one of the few methods of assessing predation intensity in fossil faunas and this reason led Dudley and Vermeij (1978) to document the drilling rates occurring in turritellid gastropods from the late Cretaceous to the present day. They concluded that the frequency of drilling had remained about the same from the Eocene until the present, but that there had been a marked increase from the late Cretaceous to the Eocene. Our data from the Black-
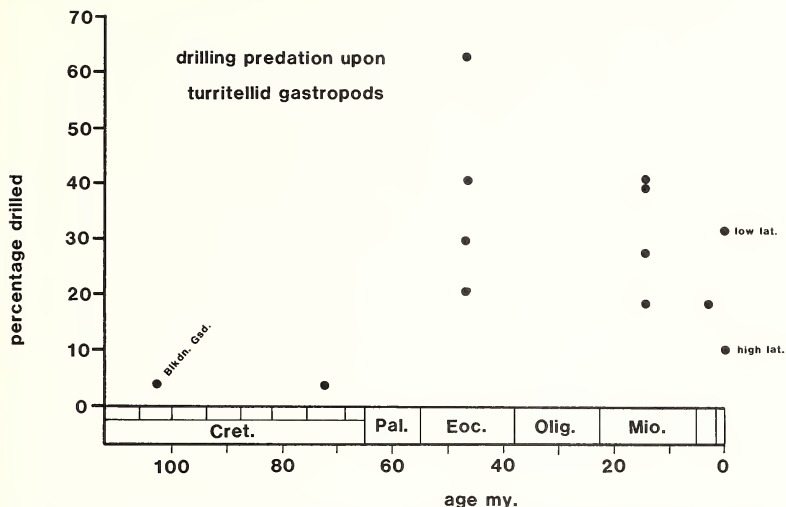
TEXT-FIG. 15. Percentage frequency of predation on turritellid gastropods from various faunas from the Cretaceous to Recent. Data from Table 6.

down Greensand giving a 3·7% drilling frequency for *Turritella* are remarkably similar to the 3·8% recorded by Dudley and Vermeij (1978) from the Campanian–Maastrichtian. Further data from the Cenozoic (Table 6) corroborate their findings that Cenozoic drilling rates upon *Turritella* were at least four or five times greater than had occurred in the Cretaceous (text-fig. 15).

We have also extracted comparable data for glycymerid and corbulid bivalves, that were abundant in the Blackdown fauna and are prominent in published accounts of Cenozoic drilling predation (Table 6). In the Glycymerididae, Albian predation rates (10%) are similar to those of the Eocene, but most post-Eocene rates are much higher (24% and above). The drilling rates in Eocene Corbulidae are about double those of the Albian but samples from post-Eocene faunas are rather limited.

When the few complete assemblages that have been analysed are compared (Table 6), it is found that the overall drilling rates on gastropods and bivalves are two to three times higher in the Cenozoic than in the Cretaceous. The predation rate of bivalves for the Eocene of Nigeria (Adegoke and Tevesz 1974) is lower than for other Cenozoic faunas and this led those authors to suggest that there had been a shift in prey preference by predators from mainly gastropods in the Eocene to predominantly bivalves at the present day. It would appear that this conclusion was based upon inadequate sampling and, perhaps, an anomalously low predation rate upon the bivalves in their fauna. To our knowledge, there are no accounts of Recent assemblages that have been analysed in the same way as the fossil faunas; Reyment (1966) examined a fauna from the Niger delta, but did not provide full details, nor give sample sizes.

Thus, both with regard to individual taxa and total assemblages, our data support the hypothesis that there has been a marked increase in drilling predation from the Cretaceous to the Cenozoic and that predation rates throughout the Cenozoic have probably been similar to those of the present day.

However, as Vermeij (1980) pointed out, there is likely to be considerable variation in predation intensity at any one time, depending upon the abundance of drilling predators, and it is apparent that such molluscs were certainly not very abundant during the Albian.

The increased success and efficiency of predators generates selection for defence mechanisms in the prey, which in turn cause selection for predation mechanisms to overcome the defences. This escalating arms race between predators and their prey has been discussed recently (see reviews by Hughes 1980a; Bayne 1981) while details of the refugia sought by the prey and the evolutionary response caused in the predator–prey interaction have been examined by Kitchell *et al.* (1981). The adaptations used by prey will tend to be morphological, chemical, or behavioural. These will include escape reactions; camouflage by colour, or morphology; selection of cryptic habitats, or living positions out of reach of the predator; patchy, or other dispersed distributions; refuge through growth beyond that likely to succumb to a successful attack by the predator; and morphological armament reducing the efficiency of attack. Some of the possible responses of prey species to the increased activities of predators in the late Cretaceous have been discussed by Stanley (1977b), Vermeij (1977), and Taylor (1981). These included on the positive side: deeper burrowing in bivalves, strengthening and armament of shells, habitat shifts; or the negative consequence of ultimate extinction. A size refuge from predation has been widely reported. In one study on *Mya arenaria*, Edwards and Huebner (1977) have demonstrated that although small and medium-sized *Mya* are heavily predated by *Polinices duplicatus*, larger individuals are seldom attacked; the reproductive reservoir of these larger molluscs which cannot be handled by *Polinices* is sufficient to maintain the *Mya* population. Similarly, Ansell (1960) found that *P. alderi* did not attack *Chamelea striatula* at sizes much above 15 mm.

Oysters are a major prey of muricid gastropods, both in the Albian and the Eocene of the Paris Basin (Taylor 1970). Both of these faunas represent sublittoral marine habitats with no evidence of other than normal salinities. However, at the present day, large populations of oysters are found in reduced or fluctuating salinity conditions, or in the intertidal zone. It is suggested that both of these habitats represent a refuge from the intense predation pressure of normal sublittoral habitats; fewer predators live in either reduced salinity, or intertidal habitats. A number of studies have demonstrated reduced feeding and reproductive activity in muricid gastropods in conditions of reduced or fluctuating salinities (reviewed in Broom 1982). At the present day most large populations of epifaunal bivalves are found in the intertidal, low salinity, or cryptic habitats, or alternatively have some adaptations such as swimming abilities (Pectinidae), or have an association with coelenterates (e.g. Pteriidae) that reduces predation intensity. By contrast, during the Cretaceous, sublittoral populations of these epifaunal bivalves including inoceramids, rudists, oysters, modiolids, and pteriids were abundant.

Although mollusc species with thick shells, strong sculpture, and tight closure might be expected to show lower drilling frequencies, no such correlation has been consistently established (Vermeij 1980). It might be thought that the low drilling frequencies occurring in the very abundant, strongly sculptured thick shells of the Blackdown Greensand Trigoniidae offered support for this contention. However, these trigoniids were probably capable of leaping actions to avoid predators, comparable to that shown by the living *Neotrigonia* and some Cardiidae (Stanley 1977a; Ansell 1969).

It is difficult to use drilling frequencies as an estimate of the contribution made by drilling predators to total prey mortality because other forms of predation can remove shells from the population, e.g. crushing predators. Green (1968) reported that although 22% of *Notospisula* shells were drilled by naticids, the snails only contributed to some 4% of the total annual mortality of the bivalves, 28% of which resulted from skate predation.

Therefore, it would seem clear that with drilling rates of only 4·5%, the predatory gastropods were not a particularly important influence in the mortality of benthic molluscs in the Blackdown Greensand fauna. It is most likely that fish and crustacea were far more important predators upon the fauna, but neither group has been preserved although both are common in other contemporaneous Albian deposits.
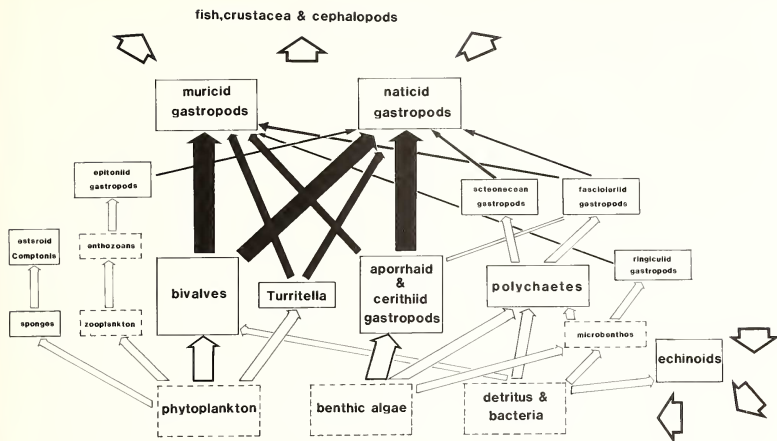
TEXT-FIG. 16. Diagrammatic reconstruction of the part of the benthic food web involving shell-drilling gastropods for the Blackdown Greensand fauna. Solid arrows indicate direct evidence of feeding relations; open arrows indicate inferred pathways. Boxes enclosed by solid lines indicate presence of fossils, dashed lines indicate inferred presence.

In order to summarize our interpretation of the Blackdown Greensand fauna, we have attempted to reconstruct part of a food web that involves the predatory gastropods (text-fig. 16). The construction of food webs for fossil faunas, obviously, has considerable limitations, in particular the inevitable lack of preservation of a large part of the fauna (see Stanton and Nelson 1980 for discussion), but it does emphasize the dynamic relationships and linkage between the various components. Our postulated food web is based upon the preserved predation evidence, a comparison with living relatives for all faunal elements, and the extrapolation of existing food webs. An instance of the evidence used can be demonstrated by the unit: all living epitoniid gastropods for which a diet is known feed upon anthozoans, these in turn feed upon zooplankton, which themselves feed upon the phytoplankton. Other units are based on similar comparisons: the asteroid *Comptonia* occurring in the Blackdown fauna belongs to the order Valvatida, Recent species of which feed upon sponges (Sloan 1980); acteonacean gastropods today feed upon polychaetes, but only a few tubiculous species are found fossil and these must represent a small fraction of the presumably prolific original fauna.

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## APPENDIX 1

*List of Bivalvia from the Blackdown Greensand and the incidence of drilling predation*

| | No. of valves V | No. of naticid drills N | No. of muricid drills M | Total no. of drills T |
|---|---|---|---|---|
| **Nuculanacea** | | | | |
| *Mesosacella angulata* (J. de C. Sowerby) | 50 | 2 | — | 2 |
| *M. lineata* (J. de C. Sowerby) | 170 | 1 | — | 1 |
| **Nuculacea** | | | | |
| *Nucula antiquata* (J. de C. Sowerby) | 224 | 4 | — | 4 |
| *N. impressa* (James Sowerby) | 143 | — | 1 | 1 |
| *N. pectinata* J. de C. Sowerby | 7 | — | — | — |
| *N. obtusa* J. de C. Sowerby | 40 | 1 | — | 1 |
| **Arcacea** | | | | |
| *Nanonavis carinatus* (James Sowerby) | 220 | — | 4 | 4 |
| *Barbatia rotundata* (J. de C. Sowerby) | 4 | — | — | — |
| *Idonearca glabra* (Parkinson) | 395 | 7 | 5 | 12 |
| *Trigonarca passyana* (d'Orbigny) | 1 | — | — | — |
| **Limopsacea** | | | | |
| *Glycymerita sublaevis* (J. de C. Sowerby) | 202 | 2 | 5 | 7 |
| *G. umbonata* (James Sowerby) | 425 | 15 | 11 | 26 |
| **Mytilacea** | | | | |
| *Falcimytilus lanceolatus* (J. de C. Sowerby) | 42 | — | 5 | 5 |
| *Musculus striatocostatus* (d'Orbigny) | 8 | — | — | — |
| *Modiolus reversa* J. de C. Sowerby | 148 | 4 | 3 | 7 |
| 'Perna' *inaequivalvis* J. de C. Sowerby | 6 | — | — | — |
| *Crenella bella* J. de C. Sowerby | 2 | — | — | — |
| *C. orbicularis* (J. de C. Sowerby) | 147 | 1 | 1 | 2 |

| | No. of valves V | No. of naticid drills N | No. of muricid drills M | Total no. of drills T |
|---|---|---|---|---|
| **Pteriacea** | | | | |
| *Inoceramus concentricus* (Parkinson) | 156 | — | — | — |
| *I. subsulcatus* Wiltshire | 7 | — | — | — |
| *I. sulcatus* Parkinson | 6 | — | — | — |
| *Gervillia forbesiana* d'Orbigny | 5 | — | — | — |
| *Gervillella sublanceolata* (d'Orbigny) | 37 | — | 1 | 1 |
| *Bakevillia rostrata* (J. de C. Sowerby) | 15 | — | 3 | 3 |
| '*Pseudoptera*' *anomala* J. de C. Sowerby | 3 | — | — | — |
| **Pectinacea** | | | | |
| *Neithea gibbosa* (Pulteney) | 53 | — | — | — |
| *N. quinquecostata* James Sowerby | 1 | — | — | — |
| *Camptonectes milleri* (J. de C. Sowerby) | 46 | — | 1 | 1 |
| *Mimachlamys robinaldinus* (d'Orbigny) | 12 | — | — | — |
| *Chlamys stutchburianus* (J. de Sowerby) | 2 | — | — | — |
| *C. elongata* (Lamarck) | 2 | — | — | — |
| *Spondylus striatus* (James Sowerby) | 2 | — | — | — |
| **Pinnacea** | | | | |
| *Pinna robinaldina* (d'Orbigny) | 6 | — | 1 | 1 |
| **Limacea** | | | | |
| *Lima elongata* J. de C. Sowerby | 1 | — | — | — |
| *L. subovalis* J. de C. Sowerby | 5 | — | — | — |
| *L. tecta* (d'Orbigny) | 1 | — | — | — |
| *Limatula fittoni* (d'Orbigny) | 3 | — | 1 | 1 |
| **Ostreacea** | | | | |
| *Amphidonte obliquata* (Pulteney) | 375 | 3 | 28 | 31 |
| *Acutostreon* sp. | 11 | — | — | — |
| **Trigoniacea** | | | | |
| *Pterotrigonia aliformis* (Parkinson) | 189 | — | — | — |
| *P. scabricola* (Lycett) | 157 | — | — | — |
| *Rutitrigonia eccentrica* (Parkinson) | 138 | 1 | 1 | 2 |
| *Oistotrigonia spinosa* (Parkinson) | 19 | — | — | — |
| *Quadratotrigonia daedala* (Parkinson) | 48 | — | 2 | 2 |
| *Q. spectabilis* (J. de C. Sowerby) | 95 | — | — | — |
| **Lucinacea** | | | | |
| '*Lucina*' *pisum* J. de C. Sowerby | 71 | 1 | — | 1 |
| '*L.*' *downesi* Woods | 8 | 1 | — | 1 |
| *Mutiella canaliculata* (J. de C. Sowerby) | 17 | 2 | — | 2 |
| *Lucina* sp. | 1 | — | — | — |
| **Crassatellacea** | | | | |
| *Nicaniella formosa* (J. de C. Sowerby) | 552 | 15 | 1 | 16 |
| *Eriphyla striata* (J. de C. Sowerby) | 17 | 1 | 2 | 3 |
| *Astarte impolitum* (J. de C. Sowerby) | 2 | — | — | — |
| **Cardiacea** | | | | |
| *Granocardium proboscideum* (James Sowerby) | 42 | — | 3? | 3 |
| *Protocardia querangeri* (d'Orbigny) | 2 | — | — | — |
| *P. hillana* (James Sowerby) | 200 | 6 | 3 | 9 |
| *Thetis laevigata* (James Sowerby) | 88 | 3 | 1 | 4 |
| *Globocardium* sp. | 2 | — | — | — |
| *Unicardium* sp. | 1 | — | — | — |

| | No. of valves V | No. of naticid drills N | No. of muricid drills M | Total no. of drills T |
|---|---|---|---|---|
| **Mactracea** | | | | |
| *Mactra angulata* J. de C. Sowerby | 156 | 1 | — | 1 |
| *Mactra* sp. | 2 | — | — | — |
| **Arcticacea** | | | | |
| *Venilicardia cuneata* (J. de C. Sowerby) | 153 | — | 2 | 2 |
| *V. lineolata* (James Sowerby) | 95 | 2 | 1 | 3 |
| *Epicyprina angulata* (James Sowerby) | 76 | 4 | 3 | 7 |
| *E. subtruncata* (d'Orbigny) | 1 | 1 | — | 1 |
| **Veneracea** | | | | |
| *Chimela caperata* (J. de C. Sowerby) | 189 | 4 | — | 4 |
| *Callistina plana* (James Sowerby) | 201 | 3 | — | 3 |
| *Flaventia ovalis* (J. de C. Sowerby) | 66 | 3 | — | 3 |
| *Paraesa faba* (J. de C. Sowerby) | 61 | 3 | — | 3 |
| *Calva subrotunda* (J. de C. Sowerby) | 42 | 1 | — | 1 |
| **Tellinacea** | | | | |
| *Palaeomoera inaequalis* (J. de C. Sowerby) | 183 | 9 | — | 9 |
| *?Linearia striatuloides* (Stoliczka) | 39 | 1 | — | 1 |
| *Linearis subtenuistriata* (d'Orbigny) | 26 | — | — | — |
| *Icanotia siliqua* Casey | 3 | — | — | — |
| *Quenstedtia pelagi* (d'Orgibny) | 2 | — | — | — |
| **Solenacea** | | | | |
| *Senis* sp. | 1 | — | — | — |
| **Myacea** | | | | |
| *Corbula elegans* J. de C. Sowerby | 712 | 42 | — | 42 |
| *C. truncata* J. de C. Sowerby | 145 | 7 | — | 7 |
| **Pholadomyacea** | | | | |
| *Panopaea mandibula* | 33 | 1 | — | 1 |
| *Goniomya mailleana* (d'Orbigny) | 4 | — | — | — |
| *Myopholas* sp. | 2 | — | — | — |
| **Thraciacea** | | | | |
| *Periplomya* cf. *simplex* (d'Orbigny) | 2 | — | — | — |
| *Platymoida cosnensis* (de Loriol) | 2 | — | — | — |
| **Poromyacea** | | | | |
| *Liopistha gigantea* (James Sowerby) | 57 | — | — | — |